

DENSITY IS ALTERED IN HYDROMEDUSAE AND CTENOPHORES IN RESPONSE TO CHANGES IN SALINITY

CLAUDIA E. MILLS

*Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington, 98250 and
Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2

ABSTRACT

Laboratory experiments have determined the behavioral and gross physiological responses of hydromedusae and ctenophores subjected to sudden changes of salinities in the range that might be encountered in nature. Nine species of hydromedusae (*Aequorea victoria*, *Aglantha digitale*, *Bougainvillia principis*, *Gonionemus vertens*, *Phialidium gregarium*, *Polyorchis penicillatus*, *Proboscoidactyla flavicirrata*, *Sarsia tubulosa*, *Stomatoca atra*) and two species of ctenophores (*Bolinopsis infundibulum*, *Pleurobrachia hachei*) were transferred from natural sea water of 30.5‰ to modified sea waters of 19–38‰. Most species altered their density within a few hours by osmoconforming to salinities ranging from 23–38‰, so that equilibrium buoyancy (either positive, neutral, or negative, according to species) was regained along with normal behavior. Even salinity differences of only 1–2‰ required 30–60 minutes adjustment time. Prior to regaining their equilibrium buoyancies, differences in relative density caused medusae and ctenophores to sink when introduced to low salinity water and to float in high salinity water. Hence, simple density differences combined with the natural intermittent swimming behavior of hydromedusae suggest that in many cases medusae may not actually be able to cross sudden density gradients. In the event that a medusa or ctenophore is moved into water of a different salinity, however, its ability to adjust will allow the animal to resume normal swimming and feeding activities within a short time.

INTRODUCTION

Medusae and ctenophores typically drift or swim weakly in the plankton. Each species has a characteristic inherent buoyancy which causes it to float, sink, or hover when at rest (Mills, 1981b). This species-specific “steady state” buoyancy (which will henceforth be referred to as equilibrium buoyancy) is presumably determined by regulation of sulphate ion within the mesoglea in combination with body construction (Mills and Vogt, 1984). The property of floating, sinking, or hovering is closely coupled with species-specific swimming and feeding behaviors of jellyfish in nature.

Most species of medusae and ctenophores have lifespans varying between several days and several months. Many species occur within rather narrow depth limits in the water column, although these depths may be modified by diel vertical migrations of up to several hundred meters (Benović, 1973; Moreira, 1973; Mills, 1982). If it is correct to assume that most jellyfish travel many miles in their lifetimes, then in many cases they will encounter waters of different salinities in their wanderings. It is of interest to determine whether these organisms are able to adapt to the range of

Received 9 May 1983; accepted 23 November 1983.

* Present address.

salinities which might be encountered in nature, or, conversely, whether variations in salinity provide a hazard to which many planktonic medusae succumb.

Recently Leonard (1980) observed that the hydromedusa *Sarsia tubulosa* is able to vary its density in order to remain positively buoyant in salinities varying from 20 to 27‰. She did not, however, distinguish between active ionic regulation of buoyancy and passive change in density due to osmotic accommodation. Mills and Vogt (1984) determined that active sulphate exclusion is an important factor in buoyancy regulation, but that ion concentrations do not vary over time in a way that might facilitate diel vertical migration of medusae and ctenophores. In the present paper, the general phenomenon of density regulation in response to changes in salinity is investigated. Several species of medusae and ctenophores with different equilibrium buoyancies have been exposed to a variety of salinities in order to determine (1) whether they can regulate their density in response to salinity changes and (2) the rate of any such adjustments.

MATERIALS AND METHODS

Field conditions

In the nearshore coastal and inland marine waters of Washington state (U. S. A.) and British Columbia (Canada), at least 60 species of hydromedusae and 11 species of ctenophores have been collected (Arai and Brinckmann-Voss, 1980; Mills, 1981a). These jellyfishes comprise a substantial component of the zooplankton from April through October; a few of the species are present year-round. The majority of species are characteristic of surface waters (Mills, 1982).

Salinity of these inland waters (which include Puget Sound, the San Juan Archipelago, and the Strait of Georgia) is usually between 28 and 31‰ although salinities from 24–35‰ are common; surface waters in some areas may drop below 15‰ during times of heavy rainfall or snowmelt (Collias and Barnes, 1966; Herlinveaux and Giovando, 1969; U. S. Dept. of Commerce, 1974). Water temperature may range from about 5° to 18°C, but in many areas the annual fluctuation is only a few degrees, temperatures averaging about 11°C.

According to Herlinveaux and colleagues (1961, 1962, 1969), a pycnocline exists throughout the year in most of these areas, with water of lower salinity near the surface. Salinity changes are more important than temperature changes in forming the pycnocline. In summer, the temperature gradient reinforces a density structure predetermined by the salinity gradient, and in winter when there is no thermal gradient, the pycnocline occurs at the halocline. The greatest drop in density occurs between 0 and 25 m; below 50 m only a small density gradient occurs year-round.

Animals

Nine species of hydromedusae (*Aequorea victoria*, *Aglantha digitale*, *Bougainvillia principis*, *Gonionemus vertens*, *Phialidium gregarium*, *Polyorchis penicillatus*, *Proboscidaactyla flavicirrata*, *Sarsia tubulosa*, *Stomatoca atra*) and two species of ctenophores (*Bolinopsis infundibulum*, *Pleurobrachia bachei*) were collected in glass or plastic beakers from surface waters near the Friday Harbor Laboratories in the San Juan Archipelago, Washington. *Gonionemus* medusae were collected in Mitchell Bay, San Juan Island, and *Polyorchis* medusae were collected in Shoal Bay, Lopez Island. All other species were collected from beside the floating docks of the Friday Harbor Laboratories. Only animals which appeared to be in excellent condition were used for the experiments.

Modified sea waters

Within a few hours of collection, the medusae or ctenophores were transferred to modified sea water in order to determine behavioral and gross physiological responses to sudden changes in salinity. The experiments were conducted in 1000 or 500 ml glass beakers maintained at ambient sea water temperature (11–14°C) by immersion in an indoor running sea water table. The contents of the beakers ranged in salinity from approximately 19‰ to 38‰ as follows: (1) 60% sea water, 40% fresh (tap) water (19‰ ± 1.0‰), (2) 75% sea water, 25% fresh water (23.0‰ ± 1.0‰), (3) 90% sea water, 10% fresh water (27.5‰ ± 1.0‰), (4) 100% sea water (30.5‰ ± 1.0‰), (5) 100% sea water plus 8 g NaCl per liter (38.0‰ ± 1.0‰). Additionally, salinities 1‰ and 2‰ below and 1‰ above ambient sea water (which will henceforth be referred to as “normal” sea water) were used with *Aequorea* and *Phialidium*. Salinities were measured with an Endeco Type 102 handheld Refractometer/Salinometer.

Depending on sizes of medusae or ctenophores, 2–12 animals of the same species were placed in a beaker together. Several sets of similar experiments were made with each species during the summer months of 1979–1982 as follows: *Aequorea victoria* (8 sets, 146 medusae total); *Aglantha digitale* (5 sets, 62 medusae total); *Bougainvillia principis* (2 sets, 60 medusae total); *Gonionemus vertens* (4 sets, 100 medusae total); *Phialidium gregarium* (6 sets, 207 medusae total); *Polyorchis penicillatus* (3 sets, 61 medusae total); *Proboscidactyla flavicirrata* (5 sets, 68 medusae total); *Sarsia tubulosa* (6 sets, 192 medusae total); *Stomatoca atra* (4 sets, 128 medusae total); *Bolinopsis infundibulum* (3 sets, 59 animals total); and *Pleurobrachia bachei* (2 sets, 44 animals total). (In each set of experiments, all salinities were used, but the numbers of animals were not always equal, subject to availability.)

The medusae and ctenophores were observed for several hours after they had been transferred to new salinities, until their buoyancy and activities returned to normal or until it was obvious that such an adjustment would not be accomplished. In many cases, the animals remained in the new salinities for as long as 48 hours, after which they were returned to natural sea water (approximately 30‰). Their reactions and ability to adjust to this second abrupt salinity change were also observed.

Mesogloal osmolarity

Because of its relatively large size, *Aequorea victoria* was chosen for measurements of the colligative properties of jellyfish mesogloea in different salinities. Osmolalities of the various dilutions of sea water and of the mesogloea of *Aequorea* were measured in order to determine whether osmotic accommodation was responsible for the change in jellyfish density that followed exposure to water of a new salinity. *Aequorea* medusae from the field were placed in 75%, 90%, 97%, 100%, and 127% sea water for 24 hours during which they adjusted to the change, regaining their normal buoyancies relative to the surrounding media. Samples of mesogloea were obtained by pushing a cork borer through the thickest portion of an *Aequorea*, where the mesogloea was about 15–20 mm thick. The exumbrellar and subumbrellar epithelia were trimmed away and the mesogloal core was then homogenized in a Pyrex tissue grinder. Freezing points of 2 ml samples of sea water or of homogenized mesogloea were measured with a Fiske Osmometer.

Isotonic Percoll experiments

Four species of medusae (*Aequorea victoria*—10 animals, *Phialidium gregarium*—26 animals, *Proboscidactyla flavicirrata*—8 animals, *Sarsia tubulosa*—10 animals)

were placed in a mixture of sea water and Percoll (Pharmacia Fine Chemicals) which changed the density, but not the tonicity of sea water. Percoll is a colloidal suspension of silica coated with polyvinyl pyrrolidone; it is nontoxic, and exhibits low osmolality, low viscosity, and high density. After preparing dialysis tubing (Brewer *et al.*, 1974), 100 ml of Percoll was dialyzed against 5 changes of 3 liters of sea water over 22 hours. The density of Percoll after dialysis was 1.148 g/ml. The density of normal sea water with salinity 31.0‰ was 1.026 g/ml and density of hypertonic sea water made by adding 8 g NaCl per liter for a final salinity of 38.5‰ was 1.034 g/ml. One part dialyzed Percoll was added to 14 parts sea water for a final density of 1.034 g/ml (all measurements at 13–15°C). Osmolalities of the above mixtures were measured on a Fiske Osmometer and found to be 800 mOsm/kg for 31.0‰ sea water, 785 mOsm/kg for Percoll-sea water (1:14 v/v) and 1146 mOsm/kg for 38.5‰ sea water.

Behavior and relative buoyancies of medusae in the Percoll-sea water mixture were observed for 24 hours. The medusae were then returned to normal sea water in order to check for any subtle adjustments in density (and relative buoyancy) that may have occurred in the Percoll-sea water mixture.

RESULTS

A standard pattern of events occurred when any species of medusa or ctenophore was introduced to water of a different salinity (Fig. 1). When placed in hypotonic sea water, the jellyfish were relatively dense. Those individuals that had been negatively buoyant or neutrally buoyant in normal sea water sank to the bottom of the experimental beakers; positively buoyant species sank if the drop in salinity

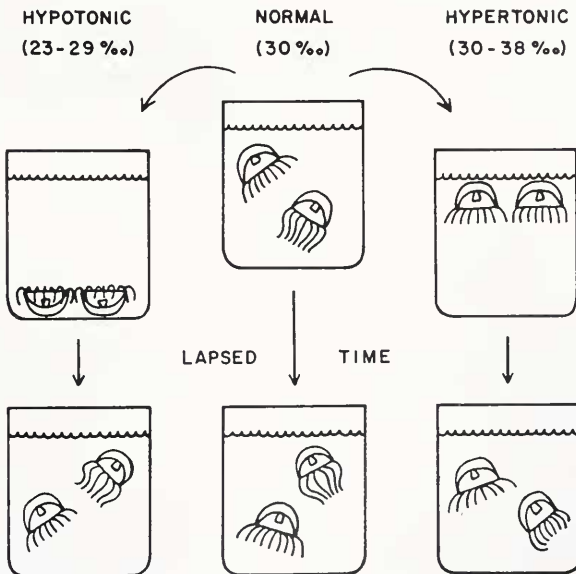


FIGURE 1. Osmotic accommodation to sea water of various salinities. Hydromedusae and ctenophores transferred from normal sea water to hyposaline sea water sink and remain on the bottom of the container even though swimming pulsations are not impaired. Conversely, animals transferred to hypersaline water float even though they, too, are able to pulsate normally. In time, animals in either hyposaline or hypersaline water adjust osmotically, regain their equilibrium buoyancy in the medium, and swim freely throughout the container.

was sufficient to compensate for their density. When placed in hypertonic sea water, all species initially floated. In addition to the change in relative buoyancy, animals placed in 60%, 75%, or 127% sea water usually responded behaviorally to the stress by contracting their bells and their tentacles; they usually ceased normal swimming pulsations for a few minutes. Eventually, in most cases, the medusae or ctenophores returned to their equilibrium buoyancies in the modified sea waters and carried out apparently normal activities.

The times required for individuals of each species to return to equilibrium buoyancy are given in Table I. Sea water diluted to 60% was lethal to most species; in such cases, individuals lay on the bottom, almost immediately ceased pulsating, and were unable to recover under any condition.

Most species accommodated within a few hours to 75% sea water, although initially the animals were relatively too dense to lift themselves off the bottom. Exceptions to this adaptability are listed below. *Aglantha* could not adjust, and indeed, usually succumbed in 75% sea water. *Phialidium* and *Aequorea* both failed to recover buoyancy and normal behavior in about one-half of the trials. *Gonionemus* usually did not behave normally in 75% sea water, but nevertheless was able to recover fully if placed back into normal sea water after 24 hours.

Sea water diluted to 90% caused a visible buoyancy problem for most species at first. Medusae were usually not able to lift off the bottom initially, but most were able to swim throughout the beaker within a few minutes. Complete return to equilibrium buoyancy in 90% sea water usually required a few hours—longer than resumption of swimming ability.

Medusae and ctenophores all floated after being introduced to hypertonic sea water of 127%, but all species (including those that are positively buoyant at equilibrium) began to sink within a few hours. It should be noted that most *Aglantha* and *Sarsia* and some *Bougainvillia* and *Phialidium* medusae never fully recovered equilibrium buoyancy and normal behavior in this high salinity water.

Even small changes in salinity caused initial sinking or floating of medusae. *Aequorea* and *Phialidium* required approximately 30–60 minutes to return to equilibrium buoyancy after being placed in water differing by only $\pm 2\text{‰}$ from normal sea water.

All medusae which had originally adjusted to hypo- or hypertonic sea water were able to readjust to normal sea water within 24 hours. The precise temporal details of this readjustment were not usually recorded.

Osmolality measurements of sea water samples and of mesogloea from 10 *Aequorea* medusae that had accommodated to the various sea water dilutions show that the osmolality of mesogloea closely corresponds over a wide range of salinities to the osmolality of the surrounding sea water (Fig. 2). In most cases these medusae were slightly hypo-osmotic to their surroundings.

All medusae placed in denser, but isotonic Percoll-sea water mixtures floated indefinitely at the surface. They were unable to swim very far below the water surface, but otherwise behaved normally for the entire 24 hour period of observation in this medium. When subsequently returned to normal sea water, all medusae immediately assumed their normal equilibrium buoyancies, confirming that no density adjustments had occurred in response to the denser Percoll-sea water medium.

DISCUSSION

These experiments demonstrate that many species of hydromedusae and ctenophores are able to adjust their buoyancies when they encounter changes in

TABLE I

Time in hours required for hydromedusae or ctenophores to adjust osmotically to water of various salinities

Species	Equilibrium buoyancy	Salinity—% of normal 30.5‰			
		60% (19‰ ± 1.0‰)	75% (23.0‰ ± 1.0‰)	90% (27.5‰ ± 1.0‰)	127% (38.0‰ ± 1.0‰)
Hydromedusae					
<i>Aequorea victoria</i>	negative	lethal; no recovery	20 or no recovery	1-5	5-10
<i>Aglantha digitale</i>	negative	lethal; no recovery	lethal; no recovery	no visible effect	1*
<i>Bougainvillia principis</i>	positive	not tested	4.5-6	1.5	1*
<i>Gonionemus vertens</i>	negative	buoyancy not recovered	24	1 or no visible effect	2-5
<i>Phialidium gregarium</i>	negative	lethal; no recovery	3 or no recovery	0.5-1.5	1-3
<i>Polyorchis penicillatus</i>	negative	6.5	7-11	2-5	3-6
<i>Proboscidactyla flavicirrata</i>	neutral	24	2-5	1-1.5	1-5
<i>Sarsia tubulosa</i>	positive	6 hours or no recovery	1-2.5	1-2	1-2*
<i>Stomatoca atra</i>	negative	lethal; no recovery	6-10	2.5-6	2.5-6
Ctenophora					
<i>Bolinopsis infundibulum</i>	negative	lethal; no recovery	3-20	3-8	3-8
<i>Pleurobrachia bachei</i>	negative	buoyancy not recovered	3-18	3-5	3-18

Animals were collected in sea water of 30.5‰ ± 1.0‰. Adjustment was measured as the resumption in new salinities of equilibrium buoyancy and normal behavior. * Indicates animals that were unable to recover their normal buoyancy, becoming heavier than normal, but otherwise behaved normally. The time listed for these animals reflects the number of hours required to change from positive to negative buoyancy.

salinity. Of the 9 hydromedusa and 2 ctenophore species tested, only *Aglantha* failed to adjust to changes of ±8‰ from 30‰ salinity. For the other species, individuals initially sink or float in the new medium depending on whether it is relatively hypo- or hypersaline; swimming behavior may be suppressed during this early period. Full buoyancy adjustment sometimes requires several hours, particularly if the salinity change is very great. Once accommodation has occurred, however, medusae and ctenophores display normal swimming and feeding activities.

Measurements of osmolality in *Aequorea mesogloea* imply that adjustment of

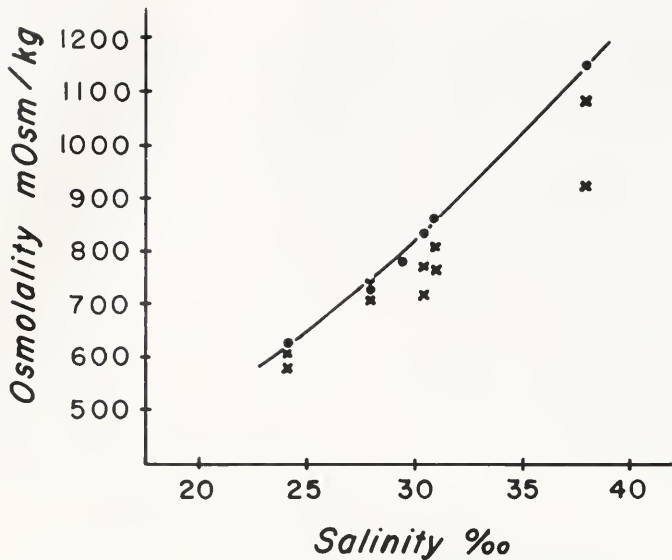


FIGURE 2. Osmolality of various dilutions of sea water (●) and of the mesogloea of 10 *Aequorea victoria* medusae (X) that had remained in the various sea water concentrations for 24 hours and regained their equilibrium buoyancies (curve is fit by eye, each point on the graph is established by two measurements of each sample).

buoyancy in this species is primarily the result of passive osmotic accommodation, *i.e.*, a mass movement of water between the inside and outside of a medusa based on osmolarity differences between the medusa and its surrounding medium. In terms of habitat, *Aequorea* is representative of those species that live in surface waters and are subject to large changes in salinity. Results with *Aequorea* probably can be extended to the other 10 species used in these experiments, but that are too small for conveniently measuring mesogloecal osmolality. (*Aglantha*, which did not readily adjust to salinity changes, lives in deep water—approximately 100 m by day. *Aglantha* is a vertical migrator, capable of moving up to the surface at night, but my results imply that *Aglantha* probably remains below any strong halocline.)

The Percoll experiments show that if sea water density is changed without altering salinity, jellyfish make no buoyancy adjustments in the medium. This is further evidence that changes in jellyfish buoyancy are not the result of active density regulation, but merely demonstrate a passive osmotic accommodation.

Changing the environment around a jellyfish in the laboratory certainly does not present the same situation as occurs when a jellyfish is moving through water with a salinity gradient, yet it allows conjecture about limitations to movement of medusae in the field. Accommodation as described above would occur if a jellyfish is suddenly confined to water of a different salinity, for instance if it is washed into a hypersaline lagoon or a diluted mixed estuary. Normally, however, in the nearshore habitats frequented by medusae and ctenophores, salinity changes are gradual or in small steps, with water of lower salinities layered over water of higher salinities.

Upon encountering stratification in the water column, the particular behavior of a jellyfish will depend on several variables: (1) steepness of the density gradient, (2) the rate of osmotic accommodation of the species, and (3) swimming behavior as

the means by which a jellyfish propels itself into waters of different densities; it should be noted that most hydromedusae swim in bursts of several pulsations alternating with periods of inactivity.

An upward-swimming jellyfish, if the difference in densities at the discontinuity is so great that the jellyfish can no longer make upward progress, will sink back down into water of a density in which it can swim. If the jellyfish is positively phototactic, it will continue to swim up to the discontinuity; the jellyfish may eventually adjust to the overlying less-saline water because of frequent brief forays into it, until it finally accommodates and can continue to move upward. If the jellyfish has no strong photopositive response, it may move randomly away from the discontinuity before accommodation occurs, or it may remain just below the discontinuity. However, if the difference in salinities is small and the jellyfish can easily penetrate the discontinuity, it may accommodate to the less dense layer while swimming through it, regaining its equilibrium buoyancy. Passively sinking or rising jellyfish in the field should tend to accumulate at salinity discontinuities of as little as 1‰ until the animals begin to swim, so long as the density difference at the discontinuity is sufficient to oppose the natural buoyancy of the jellyfish.

Several laboratory studies have reported "behavioral" aggregations of various types of planktonic animals in the vicinity of artificially constructed salinity or temperature discontinuities in small columns. Such aggregations can be explained by physical as well as behavioral factors. Arai (1973, 1976) described an active behavioral aggregation at either temperature or salinity discontinuities by 2 species of hydromedusae (*Sarsia tubulosa* and *Phialidium gregarium*) and a ctenophore (*Pleurobrachia bachei*). Such aggregation was probably at least partially attributable to density differences between the medusae or ctenophores and their surrounding media. Because Arai totaled all observations during the second ½ hour of her observation period, osmotic accommodation which may have been taking place in jellyfish near the discontinuity during this period is not apparent in the published data. Lance (1962) reported the accumulation of copepods and crab zoea on both sides of a density discontinuity in the laboratory, with an increasing ability over time to penetrate the dilute upper layer. These observations are probably due to an increase of the relative density of organisms placed in dilute sea water and an initial inability of these organisms to propel themselves through the less dense medium, followed by gradual osmotic adjustment of density. Harder (1968) observed that a variety of planktonic animals in the laboratory accumulate at regular salinity discontinuities, but do not accumulate at salinity discontinuities where a density gradient is not also present (as when sucrose is added to the overlying less-saline layer). Again, the aggregation behavior at salinity discontinuities can probably be explained in terms of relative densities and swimming abilities. Hydromedusae and ctenophores are relatively large zooplankters and their movements across discontinuities are probably a major source of small-scale mixing.

There are no reports at present documenting cases in which jellyfish were able to pass through density discontinuities in the field. Cases in which medusae have been stopped by discontinuities have seemed more intrinsically interesting. Kramp (1959) states that diurnal movements of oceanic medusae are usually barred by a discontinuity. Hansen (1951) reports that a combined temperature and salinity discontinuity in Oslo Fjord separates the hydromedusa *Sarsia tubulosa*, which occurs only in the discontinuity layer, from the hydromedusa *Aglantha digitale* and the siphonophore *Lensia conoidea*, both of which appear to diurnally migrate within the water mass below the discontinuity. Moreira (1973, 1978) reports that salinity discontinuities off Brazil limit the upward vertical migration of some species of hydro-

medusae. Furthermore, temperature discontinuities off Brazil are also effective in limiting upward movement of some cold stenohaline species characteristic of deep subtropical waters, that are unable to tolerate the warm upper layers of shelf or coastal water.

In this paper, I have not studied the effects of temperature on buoyancy, but it is assumed that except when the water temperature above the thermocline is actually lethal, density differences caused by a thermocline should be fairly easily overcome if a jellyfish can actually swim across the barrier. Having a very large surface area and small overall mass, a medusa should rapidly equilibrate to the temperature of the surrounding water.

In summary, it has been demonstrated that medusae and ctenophores are able to osmotically accommodate most changes in salinity encountered in the sea. In the course of this adjustment, they regain their equilibrium buoyancy and normal swimming and feeding activities. This osmotic adjustment of buoyancy is apparently a separate process from the species-specific determination of equilibrium buoyancy via active exclusion of sulphate ion from the mesogloea.

ACKNOWLEDGMENTS

This work was supported by a University of Victoria Graduate Fellowship. Canadian NSERC Strategic Grant #G0226 to Dr. G. O. Mackie and NSF Grant #OCE8214058. Thanks are due to G. O. Mackie, R. G. Vogt, T. E. Schroeder, and J. L. Leonard for interesting discussions during the course of the research.

LITERATURE CITED

- ARAI, M. N. 1973. Behavior of the planktonic coelenterates, *Sarsia tubulosa*, *Phialidium gregarium*, and *Pleurobrachia pileus* in salinity discontinuity layers. *J. Fish. Res. Board Can.* **30**: 1105-1110.
- ARAI, M. N. 1976. Behaviour of planktonic coelenterates in temperature and salinity discontinuity layers. Pp. 211-218 in *Coelenterate Ecology and Behavior*, G. O. Mackie, ed. Plenum Press, New York.
- ARAI, M. N., AND A. BRINCKMANN-VOSS. 1980. Hydromedusae of British Columbia and Puget Sound. *Can. Bull. Fish. Aquat. Sci.* **204**: 192 pp.
- BENOVIĆ, A. 1973. Diurnal vertical migration of *Solmissus albescens* (Hydromedusae) in the southern Adriatic. *Mar. Biol.* **18**: 298-301.
- BREWER, J. M., A. J. PESCE, AND R. B. ASHWORTH. 1974. *Experimental Techniques in Biochemistry*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 374 pp.
- COLLIAS, E. E., AND C. A. BARNES. 1966. Physical and chemical data for Puget Sound and approaches January 1960-December 1961. *Univ. Wash. Dept. Oceanogr. Tech. Rep.* **114**: 286 pp.
- HANSEN, K. V. 1951. On the diurnal migration of zooplankton in relation to the discontinuity layer. *J. Cons. Cons. Int. Explor. Mer* **17**: 231-241.
- HARDER, W. 1968. Reactions of plankton animals to water stratification. *Limnol. Oceanogr.* **13**: 156-168.
- HERLINVEAUX, R. H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. *J. Fish. Res. Board Can.* **19**: 1-37.
- HERLINVEAUX, R. H., AND L. F. GIOVANDO. 1969. Some oceanographic features of the inside passage between Vancouver Island and the mainland of British Columbia. *Fish. Res. Board Can. Tech. Rep.* **142**: 48 pp.
- HERLINVEAUX, R. H., AND J. P. TULLY. 1961. Some oceanographic features of Juan de Fuca Strait. *J. Fish. Res. Board Can.* **18**: 1027-1071.
- KRAMP, P. L. 1959. The hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Rep.* **46**: 283 pp.
- LANCE, J. 1962. Effects of water of reduced salinity on the vertical migration of zooplankton. *J. Mar. Biol. Assoc. U. K.* **42**: 131-154.
- LEONARD, J. L. 1980. Density regulation in *Sarsia tubulosa* (Hydrozoa). *Helgol. Meeresunters.* **34**: 55-59.

- MILLS, C. E. 1981a. Seasonal occurrence of planktonic medusae and ctenophores in the San Juan Archipelago (NE Pacific). *Wasmann J. Biol.* **39**: 6-29.
- MILLS, C. E. 1981b. Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. *Mar. Biol.* **64**: 185-189.
- MILLS, C. E. 1982. *Patterns and Mechanisms of Vertical Distribution of Medusae and Ctenophores*. Ph.D. Dissertation, University of Victoria, Victoria, British Columbia.
- MILLS, C. E., AND R. G. VOGT. 1984. Evidence that ion regulation in hydromedusae and ctenophores does not facilitate vertical migration. *Biol. Bull.* **166**: 216-227.
- MOREIRA, G. S. 1973. On the diurnal vertical migration of hydromedusae off Santos, Brazil. *Publ. Seto Mar. Biol. Lab.* **20**: 537-566.
- MOREIRA, G. S. 1978. A preliminary laboratory study on the salinity and temperature tolerances of some medusae from the São Paulo Coast, Brazil. *Bolm. Inst. Oceanogr. São Paulo* **27**: 45-55.
- U. S. Dept. of Commerce, National Oceanic and Atmospheric Administration. 1974. *Key to Oceanographic Records Documentation No. 2. Temperature, Salinity, Oxygen, and Phosphate in Waters off United States. Vol. III. Eastern North Pacific*. Environmental Data Service, Washington, DC. 259 pp.